Early Silurian oceanic episodes and events

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Abstract: Biotic cycles in the early Silurian correlate broadly with postulated sea-level changes, but are better explained by a model that involves episodic changes in oceanic state. Primo episodes were characterized by cool high-latitude climates, cold oceanic bottom waters, and high nutrient supply which supported abundant and diverse planktonic communities. Secundo episodes were characterized by warmer high-latitude climates, salinity-dense oceanic bottom waters, low diversity planktonic communities, and carbonate formation in shallow waters. Extinction events occurred between primo and secundo episodes, with stepwise extinctions of taxa reflecting fluctuating conditions during the transition period. The pattern of turnover shown by conodont faunas, together with sedimentological information and data from other fossil groups, permit the identification of two cycles in the Llandovery to earliest Wenlock interval. The episodes and events within these cycles are named: the Spirodden Secundo episode, the Jong Primo episode, the Sandvika event, the Malmøykalven Secundo episode, the Snipklint Primo episode, and the Ireviken event.

Oceanic and climatic cyclicity is being increasingly recognized in the geological record, and linked to major and minor sedimentological and biotic fluctuations. A model for oceanic changes has been developed by Jeppsson (1988, 1990), who tested its predictions on Palaeozoic sequences, with particular reference to Silurian sediments and conodont faunas. Here we extend these observations to document more fully the pattern of early Silurian episodes and events, and to relate it to the oceanic model.

The suggestion of cyclicity in the early Palaeozoic is not new. McKerrow (1979) used changes in sedimentary facies and brachiopod-dominated benthic communities to propose a pattern of cyclic changes in sea level, and the same approach has subsequently been taken in a number of more specific studies of Silurian sea-level fluctuations (e.g. Johnson et al. 1981, 1985, 1991a; Johnson & Worsley 1982; Johnson 1987). Leggett et al. (1981) added evidence from black shale distribution and from graptolite and brachiopod diversity trends to suggest an alternation between polytaxic, greenhouse conditions and oligotaxic, oxygenated conditions. Their recognition of three greenhouse phases in the Cambrian to Silurian addresses a broader scale of cyclicity than considered here. Within the Silurian, Schönlaub (1986) related Silurian lithological and faunal changes causally to sea-level fluctuations. Similarly, Chatterton et al. (1990) related appearances and disappearances of Llandovery and Wenlock trilobite and conodont clades in northwestern Canada to transgressive–regressive events. They identified four intervals of comparatively high extinction and/or emigration rate, each coinciding with the onset of a sedimentary change interpreted as reflecting transgression or regression. An overview of the evidence for eustatic sea-level changes in the Silurian was presented by Johnson et al. (1991b), who reiterated their methodology for recognizing bathymetric change as keyed mainly to stratigraphical replacement patterns in brachiopod-dominated communities bracketed by shallower coral–stromatoporoid and deeper high-diversity graptolite as-

semblages (Johnson et al. 1991b, p. 145). Using this approach, they were able to detect four cycles within the Llandovery, each possibly lasting 2.5 Ma, with further high-stands during mid–Wenlock, early Ludlow and late Ludlow times.

As pointed out by Jeppsson (1990), models involving only habitat displacement are inadequate to explain the widespread biotic changes that are recognized in the Silurian fossil record. Further, the plots provided by Chatterton et al. (1990, figs 4 & 5) show that, in some cases, the faunal turnovers preceded the interpreted changes in depth. Thus, the correlation between sea-level variation and biotic events may not necessarily be causal, but each may record a response to a change in global climate and/or oceanic state. Caution should be used in inferring sea-level fluctuations directly from changes in benthic communities. While these communities have been demonstrated to be depth-related (e.g. Ziegler et al. 1968), they are unlikely to have been depth-specific (e.g. Bolton 1990). Their distribution will have been affected by many environmental parameters, including energy state, nutrient supply, clastic input, oxygen concentration, and light penetration, all of which can vary in response to climatic change without any variation in sea-level. A similar argument applies to the distribution of sedimentary lithologies.

Within the model developed by Jeppsson (1990), two major types of alternating oceanic state were recognized: P episodes (here termed 'primo') and S episodes (here termed 'secundo'). Abrupt changes between or within episodes, often leading to extinctions, are here termed 'events'. Each event includes two or more datum points where disappearances and/or appearances of taxa occur.

Primo episodes may be identified by a net reduction of carbonate deposition in marginal epeiric and other carbonate blankets, an increase in the clay content of these carbonates, and the occurrence of abundant and diverse communities of planktonic organisms and of those communities supported by planktonic production. Special-

ized taxa became widespread in these communities. Secundo episodes, in contrast, are characterized by pure carbonates in shallow waters, perhaps with extensive reefs, and by rich and diverse benthic faunas. Planktonic communities, and animal communities directly dependent on them, show low abundance and low diversity during secundo episodes.

The contrasts between primo and secundo episodes are interpreted as primarily due to climatic differences, linked with changes in atmospheric CO_2 concentration. The principal control is the higher storage capacity for CO_2 of the cold oceanic bottom waters of a primo episode compared with the saline bottom waters of a secundo episode. The deep water changes connected with the onset of a primo episode result in extraction of a considerable amount of CO_2 from the atmosphere. Changes associated with the onset of a secundo episode result in release of CO_2 to the atmosphere. The erosional, depositional and biological characteristics of each episode gradually restore the atmospheric CO_2 concentration to a level where a minor climatic perturbation can instigate a change in regime. Other factors may affect the global CO_2 balance. Worsley & Kidder (1991) have shown how relative emergence of land and continental palaeogeography effect a first-order control on atmospheric CO_2 levels and, hence, on climate. The time-scale of these changes is much broader than addressed here, although they may exert an influence on the duration of some primo and secundo episodes. The importance of the relative development of carbonate banks and reefs in controlling shorter-term fluctuations in atmospheric CO_2 has recently been reiterated by Opdyke & Walker (1992).

The length of any episode depends on the balance between global input and output of oceanic CO_2. The numerical time-scale of Harland *et al.* (1990) gives a duration for the Llandovery Epoch of 8–9 Ma, suggesting an average duration for the early Silurian episodes of a little over 2 Ma. If relative sediment thickness is taken as a guide, the Spirodden Secundo episode was the longest in the early Silurian, spanning perhaps about 4 Ma. This accords with the interpolated numerical ages for the Silurian stage boundaries given by Harland *et al.* (1990).

The model predicts that events occurred between primo and secundo episodes when formation of new bottom water ceased or became intermittent. New water of sufficient density to replace existing bottom water was not being produced, with a resulting drop in deep upwelling and extinction or replacement in planktonic communities. P–S events ended when the density of the bottom water was sufficiently lowered, probably through geothermal heat flow, to allow circulation to recommence. The change from a secundo to a primo episode would not normally have involved any interruption in vertical circulation and the effects on the biota are less abrupt. The duration of P–S events depends upon the effects of Milankovitch cycles, but part of the early Wenlock Ireviken event has been calculated as about 90 000 years (Jeppsson 1990, based on oceanic heating data given by Worthington 1968 and ocean volume data from Bralower & Thierstein 1984).

P–S events are identified by extinctions and replacements, although the apparent severity of any event is strongly influenced by the history of the biota, as previous events may have removed many vulnerable taxa. Lithological changes at the beginning of an event are minor and gradual, whereas the end is abrupt and often marked by a very rapid change to pure carbonates in areas of carbonate deposition.

A very similar model of oceanic episodes to that of Jeppsson (1990) has been advanced by Tucker (1992, pp. 662–663), who applied the terms 'icehouse/coldhouse' and 'greenhouse' to the two states we have termed primo and secundo. Icehouse and greenhouse phases have been widely reported at a much longer time-scale (of the order of 100 Ma) than considered here, and an independent terminology is preferable for the shorter-term episodes.

In our study of Silurian biotic changes, we have placed primary reliance on long-ranging conodont lineages that appear to have been very strongly influenced by the fluctuating conditions. These appear and disappear repeatedly from the record, suggesting that they survived in refugia during adverse episodes. Such recurrent Lazarus taxa help to distinguish lithological changes due to local fluctuations from those controlled by global oceanic cycles.

In the genus *Panderodus*, one species, *P. equicostatus* (Rhodes *sensu* Jeppsson 1983), was usually abundant during secundo episodes, when it was often the only common representative of the genus. Primo episodes were contrastingly characterized by a diverse panderodontid fauna, containing many or all of *P. unicostatus* (Branson & Mehl), *P. serratus* Rexroad, *P. recurvatus* (Rhodes), *P. langkawiensis* (Igo & Koike), *P. greenlandensis* Armstrong, *P.* sp. b of Jeppsson (1987), and sometimes also *P. equicostatus*. Another useful group of closely related lineages of *Ozarkodina* includes *O. aldridgei* Uyeno–*O. bohemica* (Walliser)–*O. snajdri* (Walliser), *O. sagitta rhenana* (Walliser)–*O. s. sagitta* (Walliser), *O. oldhamensis* (Rexroad), *O.* aff. *scanica* Jeppsson, *O. wimani* Jeppsson, *O. hassi* (Pollock *et al.*)–*O. gulletensis* (Aldridge)–*O. hadra* (Nicoll & Rexroad), all of which are typical of secundo episodes.

Many platform-equipped taxa, for example species of *Pranognathus*, *Pterospathodus*, *Apsidognathus* and *Aulacognathus*, are typical of primo episodes, but few lineages persisted long enough to be used as indicators of oceanic conditions through several such episodes. Some conodont species were widespread during both primo and secundo episodes, and others may have changed their tolerances through time.

Early Silurian conodont faunal changes are recognized over a wide area. The episodes and events they record are documented here with reference to particular successions where the stratigraphy is well known, sedimentation was fairly continuous, and exposures are good. The reference area for the episodes and events of the Rhuddanian, Aeronian and lowest Telychian (pre-*P. celloni* Biozone) stages of the Llandovery is the Oslo–Asker district of Norway. Composite stratigraphical logs of the successions on Malmøya and Malmøykalven (Oslo district), and at Spirodden and Kampebråten (Asker district) were figured by Johnson *et al.* (1991a). The reference succession for Wenlock episodes and events currently under investigation is on the island of Gotland, Sweden, which is also adopted herein for the uppermost Llandovery. The pattern of episodes and events is shown in Fig. 1 together with names derived from the reference areas. For each episode and event, we record information on boundaries and a description of lithological and faunal characteristics in the reference area. The data given for the boundaries are guides to identification and not definitions; the episodes and events can be defined only by reference to oceanic changes and not
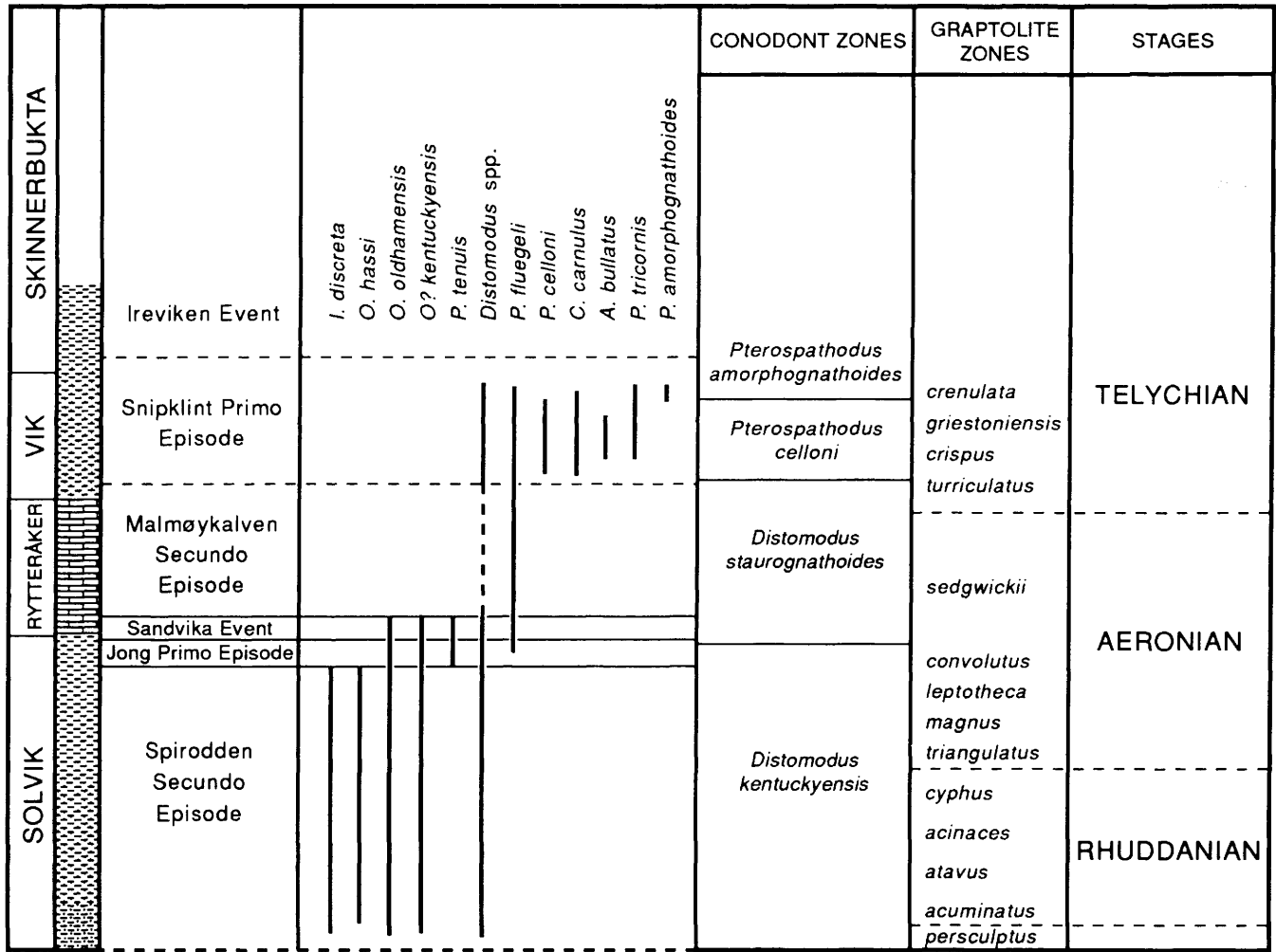
Figure 1 chart content:

Lithostratigraphical formations (left column): SKINNERBUKTA, VIK, RYTTERÅKER, SOLVIK

Episodes and events:
- Ireviken Event
- Snipklint Primo Episode
- Malmøykalven Secundo Episode
- Sandvika Event
- Jong Primo Episode
- Spirodden Secundo Episode

Key conodont species (range columns): I. discreta; O. hassi; O. oldhamensis; O? kentuckyensis; P. tenuis; Distomodus spp.; P. fluegeli; P. celloni; C. carnulus; A. bullatus; P. tricornis; P. amorphognathoides

CONODONT ZONES	GRAPTOLITE ZONES	STAGES
Pterospathodus amorphognathoides	crenulata	TELYCHIAN
Pterospathodus celloni	griestoniensis	TELYCHIAN
	crispus	
	turriculatus	
Distomodus staurognathoides	sedgwickii	AERONIAN
	convolutus	
Distomodus kentuckyensis	leptotheca	
	magnus	
	triangulatus	
	cyphus	RHUDDANIAN
	acinaces	
	atavus	
	acuminatus	
	persculptus	

Fig. 1. Early Silurian episodes and events related to chronostratigraphical divisions, conodont and graptolite biostratigraphy, and the lithostratigraphical succession in the Oslo–Asker district, Norway. Approximately to scale; Solvik Formation 190 m, Rytteråker Formation 65 m, Vik Formation 60 m. Ranges of key conodonts for the Solvik Formation based primarily on sections in Asker; for the Rytteråker Formation on sections in Asker and Malmøykalven, Oslo; for the Vik Formation on Malmøya, Oslo. Conodont data taken from Aldridge & Mohamed (1982), Idris (1984), Nakrem (1986) and unpublished collections made by R.J.A. Conodont-bearing samples have not been collected from the uppermost Vik Formation or the Skinnerbukta Formation.

by their effects on local sequences. We also give an indication of the development of each episode and event in other parts of the world; the information presented here is necessarily selective, for reasons of space and the limitations of published data. We hope, however, that we have provided an adequate outline for scientists with experience and knowledge of other successions to use their data to test our proposals rigorously.

The pattern we describe is well explained by the model, which was originally developed to understand some of the changes we are documenting (Jeppsson 1975, 1984, 1987, 1990). However, the pattern and the model can be tested independently, and we have tried to separate descriptive and interpretative aspects in our presentation. We emphasize that the pattern of episodes we have recognized does not match directly with proposed transgressive-regressive cycles, although sea-level changes will also be reflected in local successions.

The cyclicity we report here follows a period of severe faunal extinctions in the latest Ordovician, probably linked to the contemporaneous glaciation (e.g. Berry & Boucot 1973; Sheehan 1973; Brenchley & Newall 1984; Barnes 1986). These effects are evident, as elsewhere, in the upper Ordovician of the Oslo–Asker district of Norway (e.g. Brenchley & Cullen 1984). At Konglungø, near Asker (grid reference NM 849 347), shales of the Solvik Formation lie with a sharp contact on the Ordovician Langøyene Sandstone Formation (Worsley et al. 1983), and although there is no angular discordance there is probably a depositional break. The bulk of the Solvik Formation is of Rhuddanian age, but graptolites suggest that the latest Ordovician G. persculptus Biozone may be represented in the lowermost beds of the formation on the island of Ormøya, near Oslo (Howe 1982; Worsley et al. 1983, p. 16).

The Ordovician-Silurian boundary probably falls within the lower beds of the Solvik Formation at Asker rather than at the base.

The Spirodden Secundo episode

Name

After the peninsula of Spirodden, 1.6 km E of Asker, near Oslo, Norway; grid reference NM 8395 3390.

Boundaries

The onset of the episode is recognized by the first appearance of *O. hassi* and/or *O. oldhamensis* and may be of latest Ordovician (*G. persculptus* Biozone) age. In the Asker district the boundary is at or a little above the base of the Solvik Formation; *O. oldhamensis* occurs in the lowest conodont-bearing sample 8.0 m above the base at Konglungø (Aldridge & Mohamed 1982). The end of the episode coincides with the beginning of the Jong Primo episode. The Spirodden Secundo episode is represented through most of the Solvik Formation, which is approximately 190 m thick in its type area (Worsley *et al.* 1983).

Lithological characteristics in the Oslo–Asker district

Shale is dominant, but very thin to thin siltstone and limestone beds are frequent, especially in the Asker district (Worsley *et al.* 1983). Full lithological descriptions and sedimentological interpretations were given by Baarli (1985), who suggested that the strongly-bioturbated fine limestone beds were likely to represent the daily in situ deposits of tranquil environments, while the muds were introduced because of minor tectonic adjustments in the source area or as distal storm deposits.

Conodont fauna in the Oslo–Asker district

Idris (1984) listed the commoner species as *Distomodus kentuckyensis* Branson & Branson, *Icriodella deflecta* Aldridge, *Icriodella discreta* Pollock *et al.*, *Oulodus*? *kentuckyensis* (Branson & Branson), *Oulodus*? cf. *nathani* McCracken & Barnes, *Oulodus* sp. nov., *Ozarkodina protexcavata* Cooper, *O. hassi*, *O. oldhamensis*, '*Rotundacodina*' (=*Dentacodina*) cf. *dubia* (Rhodes), *Panderodus gibber* Nowlan & Barnes, *P. recurvatus*, *P. unicostatus*, *Pseudooneotodus beckmanni* (Bischoff & Sannemann) and *Walliserodus curvatus* (Branson & Branson). Thermal alteration has blackened all specimens (Aldridge 1984), making the assignment of some elements of *Panderodus* uncertain. Sporadic specimens of *Dapsilodus obliquicostatus* (Branson & Mehl) occur low in the Solvik Formation (Idris 1983), and *Coryssognathus*? sp. nov. appears towards the top (Aldridge & Mohamed 1982, pl. 1, fig. 33).

Other biota in the Oslo–Asker district

Graptolites are not abundant in the Solvik Formation, although a number of graptolitic horizons with very low-diversity climacograptid faunas have been found in the lower part; higher in the formation graptolites become rare

(Howe 1982). Acritarchs have not been investigated in the Solvik Formation. However, in the coeval Saelabonn Formation of the nearby Ringerike district, Smelror (1987) reported low acritarch species diversity and low density of individuals in strata referable to the Spirodden Secundo episode.

Benthic faunas are rather more diverse. Varied brachiopod assemblages occur throughout the Solvik Formation, although there are marked faunal turnovers at three levels (Thomsen & Baarli 1982, figs 2 & 3). Coral faunas are rich, with diversity increasing up the sequence (Neuman 1982; Aarhus 1982), a varied quiet water bryozoan fauna occurs (Spjeldnaes 1982), and trilobites are also diverse in the upper Myen and Padda members (Helbert *et al.* 1982).

Other areas

Conodont faunas of very similar composition to those from the Oslo-Asker region are widespread in Rhuddanian and lower Aeronian strata; records include North America (Branson & Branson 1947; Rexroad 1967; Cooper 1975; Fåhraeus & Barnes 1981; McCracken & Barnes 1981; Nowlan 1983; Over & Chatterton 1987) and Britain (Aldridge 1972, 1985). In North Greenland, *Icriodella* is absent and *Distomodus* is rare (Armstrong 1990), but the impoverished fauna has, as additional species, *Kockelella manitoulinensis* (Pollock *et al.*) and *Pseudolonchodina expansa* (Armstrong). The most diverse early Llandovery conodont collection is that reported from the upper Rhuddanian of New South Wales, Australia, by Bischoff (1986), where several new, possibly endemic, species of *Distomodus*, *Oulodus* and *Ozarkodina* have been identified. Armstrong (pers. comm.) has undertaken an analysis of lower Silurian conodont sequences using graphical correlation, and has independently identified conodont appearance/extinction events at the beginning and end of the Spirodden Secundo episode. He has also recognized other radiation events within the Rhuddanian, which may indicate that more than one secundo episode should be distinguished, although these events are possibly artefacts of the graphical correlation method.

The sparsity of graptolites in the Oslo sections is not matched elsewhere, and the diversity peak recognized in the *M. triangulatus* Biozone by Koren & Rickards (1980) may also indicate that the Spirodden Secundo episode could be subdivided. Acritarchs recorded from the Rhuddanian are of generally low diversity in open shelf areas. An overall increase in acritarch diversity through the stage was recorded by Hill (1974) and Hill & Dorning (1984) in the southern type Llandovery area in South Wales, although there may be some punctuation of this pattern linked to depositional sequences.

On Anticosti Island, carbonate deposition characterizes the entire episode, with bioherms developed at the base of the Silurian (Petryk 1981). The benthic biota is highly varied throughout, with diverse brachiopods, crinoids, bryozoans, corals, stromatoporoids, ostracodes and algae (Petryk 1981). Preliminary acritarch results (Duffield & Legault 1981; A. Fielding pers. comm.) indicate a low abundance and diversity of acritarchs in the Becscie Formation (Rhuddanian), with a rise in both in the succeeding Gun River Formation. Important genera in the Becscie Formation are *Diexallophasis*, *Estiastra* and *Hogklintia*.

Interpretation

For conodonts, this was a period of stasis following the late Ordovician extinctions. As is typical for secundo episodes, species with platforms, apart from the hardy *Distomodus* and *Icriodella,* are virtually unknown. Acritarchs are not well known from this interval, but the limited data available suggest a conservative microflora with a low global abundance and diversity, which is an indirect indication of low planktonic productivity. Shelf sequences around Laurentia show the carbonate deposition that is typical for secundo episodes, although there is a relative scarcity of reefs.

It is probable that this secundo episode differed somewhat in character from those later in the Silurian, as conditions may have been relatively cool. Carbonate production was less extensive globally than in subsequent secundo episodes, limiting this important sink for CO_2. This may have allowed high levels of CO_2 to persist in the ocean and the atmosphere, prolonging the time before atmospheric levels fell sufficiently for a change to primo conditions to be triggered. This would explain the relatively long duration of the Spirodden Secundo episode compared with the succeeding Jong Primo episode.

The Jong Primo episode

Name

After Jong Railway Station. Strata representing the episode are well-exposed at the Solhaugveien road section, 7.2 km NNE of Asker (Worsley *et al.* 1982, p. 164, fig. 3; grid reference NM 844 401).

Boundaries

The onset of the episode is recognized by the first appearance of the conodont *Pranognathus tenuis* (Aldridge); in Asker, this occurs 11.5 m below the top of the Solvik Formation (Aldridge & Mohamed 1982). The end coincides with the beginning of the Sandvika event.

Lithological characteristics in the Oslo–Asker district

The uppermost Solvik Formation does not differ greatly in overall character from the beds below, although the onset of the Jong Primo episode coincides with an increasing dominance of shale and a drop in the frequency of silt, sandstone and coarse bioclastic interbeds (Baarli 1985, fig. 4).

Conodont fauna in the Oslo–Asker district

The major change is the influx of abundant *Pranognathus tenuis*, although *I. discreta, I. deflecta* and *O. hassi* do not continue from the fauna of the beds below and *P. recurvatus* becomes more common (Aldridge & Mohamed 1982). *Panderodus serratus* occurs in some samples and *D. kentuckyensis* is replaced by *D.* aff. *staurognathoides* (Walliser).

Other biota in the Oslo–Asker district

Graptolites do not appear to have been recorded at this level, but acritarchs show a significant diversification in the upper part of the Saelabonn Formation of the Ringerike district (Smelror 1987, figs 4 & 6). Correlation is not yet sufficiently precise to show whether this interval of high acritarch diversity definitely coincides with the Jong Primo episode. Benthic communities in the uppermost Solvik Formation show no major change from those immediately below (Baarli 1987).

Other areas

Conodont faunas with *P. tenuis* or related species of *Pranognathus* are widespread. In Britain, they occur in the argillaceous lowermost Pentamerus Beds south of Church Stretton, Shropshire (Plowden and Marshbrook localities of Aldridge 1972) and in undescribed collections (RJA) from the upper part of the Skomer Volcanic Group of Marloes Bay, Dyfed, SW Wales. *Pranognathus tenuis* is abundant at both localities, and associated elements of the diverse faunas include *Kockelella abrupta* (Aldridge), *Dentacodina* sp., *Distomodus* aff. *staurognathoides,* *Oulodus* spp., *Pseudooneotodus* sp., *Panderodus recurvatus* and *P. serratus*; *I. deflecta, O. oldhamensis, O. hassi* and other species characteristic of the preceding episode also continue in small numbers. The range of *P. tenuis* partly coincides with the *M. convolutus* Biozone (Aldridge 1975), an interval rich in graptolites (Rickards 1976).

Contemporaneous strata in parts of North America contain *Pranognathus siluricus* (Pollock *et al.*) and *P. posteritenuis* (Uyeno). On Anticosti Island, *P. posteritenuis* occurs through the argillaceous lower half of the Jupiter Formation (Uyeno & Barnes 1983), together with *Ozarkodina pirata* (Uyeno), *Panderodus serratus* and long-ranging species. The Jupiter Formation also contains diverse acritarchs and chitinozoans (Duffield & Legault 1981; Achab 1981).

Interpretation

The Jong Primo episode is marked by the development of argillaceous sediments in areas where the succeeding Malmøykalven Secundo episode is characterized by carbonates (e.g. the Oslo Region, Welsh Borderland). Although correlations between shelly and graptolitic sequences are not yet precise, the diversification of conodonts was apparently accompanied by an enrichment of assemblages of acritarchs, chitinozoans and graptolites. These features point to an increase in overall planktonic diversity, typical of a primo episode.

The Sandvika P–S event

Name

After Sandvika, Asker district, 1 km E of Jong Railway Station; the boundary between the Solvik and Rytteråker Formations is exposed in the Solhaugveien road-cut (see Worsley *et al.* 1982) and other exposures in this area.

Lithological characteristics in the Oslo–Asker district

The lithological change from the Solvik Formation is gradational, with the lower beds of the Rytteråker Formation comprising interbedded limestones and shales. Many of these lower limestone bands are nodular and

include thalassinoidid burrow infills, although thin bioclastic bands occur and increase in importance upwards (Worsley *et al.* 1982). The limestone beds thicken and coarsen upwards in the lower part of the Rytteråker Formation.

Conodonts in the Oslo–Asker district

Pranognathus tenuis ranges into the basal beds of the Rytteråker Formation in Asker, Oslo and Ringerike, but disappears with the development of the typical limestone lithologies of the formation; most other species of the Jong Primo episode are also lost close to the Solvik–Rytteråker boundary (Aldridge & Mohamed 1982). The dominance of indurated shale and siltstone in the uppermost Solvik Formation precludes very detailed sampling for conodonts, so the boundaries of the event are difficult to recognize and a sequence of datums has not been determined. The last *O. oldhamensis* and species of *Oulodus* are from the same level as the last *P. tenuis*, and elements of *Distomodus* occur only sporadically in higher parts of the Rytteråker Formation.

Other biota in the Oslo–Asker district

The boundary between the Solvik and Rytteråker formations also marks a significant change in faunas of trilobites (Helbert *et al.* 1982) and brachiopods (Thomsen & Baarli 1982; Cocks & Baarli 1982). Representative species of both groups are different in the two formations, and both become less abundant and diverse in the Rytteråker. Graptolites have not been found at this level in the Oslo Region. In the Ringerike district the acritarch microflora changes distinctively at the base of the Rytteråker Formation. Several species, including *Leiofusa tumida* Downie and *Micrhystridium* sp. SA of Smelror (1987), have their last local occurrences at the top of the underlying Saelabonn Formation, while others, such as *Oppilatala* cf. *eoplanktonica* (Eisenack) Dorning, *Tunisphaeridium tentaculaferum* (Martin) Cramer and several species of *Veryhachium*, disappear temporarily, to reappear near the top of the Rytteråker Formation or in the overlying Vik Formation (Smelror 1987).

Other areas

In Britain, the last specimens of *P. tenuis* occur in the Pentamerus Beds of Shropshire, where they are associated with the brachiopod *Eocoelia hemisphaerica* of late Aeronian age (Aldridge 1972). *I. deflecta* and *K. abrupta* disappear close to this datum, although *O. oldhamensis* and *O. hassi* persist into younger strata (Aldridge 1985). Acritarch data are limited, but in the type Llandovery area the extinction of *Oppilatala* cf. *eoplanktonica* is recognized at the base of the *Dactylofusa estillis* Acritarch Biozone, with other taxa disappearing or appearing at the same horizon (Hill & Dorning 1984). The turnover in the microflora here, however, is not nearly as marked as that recorded in the Oslo Region. Correlations suggest that the Sandvika event occurred within the *M. sedgwickii* Biozone, a time of important evolutionary turnover in graptolite faunas (Rickards 1976). A diversity trough in British graptolite faunas within the *M. sedgwickii* Biozone is shown in the plots of Leggett *et al.* (1981).

On Severnaya Zemlya, *P. tenuis* and *Icriodella* cf. *deflecta* disappear in the middle of the Vodopad Formation, but there is no information on other biota (Männik 1983).

On Anticosti Island, the last definite *P. posteritenuis* and *O. pirata* occur in limestones about 80 m above the base of the Jupiter Formation, while the first *Ozarkodina aldridgei* were found about 12 m lower (Uyeno & Barnes 1983); again, detailed information on associated biota is limited and correlations cannot be confidently established with sequences containing *P. tenuis*. Indeed, the Sandvika event could be represented low in the Jupiter Formation where *Pranognathus siluricus* has its only record and specimens identified as *D. staurognathoides* by Uyeno & Barnes (1983) first occur; the top of the *T. tentaculaferum* Acritarch Biozone also occurs at this level (Duffield, cited in Barnes 1989).

An extinction event affecting conodonts and trilobites was recognized by Chatterton *et al.* (1990) in the late Aeronian of the Mackenzie Mountains, northwestern Canada. The conodont taxa lost include *O. oldhamensis*, *O? kentuckyensis*, *O? nathani*, *I. discreta* and *D. kentuckyensis*, while *O. hassi* disappears temporarily from the sequence (Over & Chatterton 1987). Although *P. tenuis* does not occur in the Mackenzie Mountains, it seems probable that these extinctions represent the Sandvika event. Chatterton *et al.* (1990) noted that 23% of the conodont and trilobite taxa apparently became extinct at this level, while an additional 47% disappeared to return later.

Interpretation

Sections recording the Sandvika event have not been sampled in the same detail as those of the Ireviken event, but there is clear evidence of a series of extinctions affecting several groups of organisms, coincident with a change from primo to secundo conditions.

The Malmøykalven Secundo episode

Name

After the small island of Malmøykalven, 5.5 km S of Oslo city centre, where limestones of the Rytteråker Formation are well exposed.

Boundaries

The onset of the episode is recognized by the extinction of *P. tenuis*, which in the Asker and Oslo districts is represented within the lowest 10 m of the Rytteråker Formation. The end coincides with the beginning of the Snipklint Primo episode, within the lowest part of the overlying Vik Formation.

Lithological characteristics in the Oslo–Asker district

The Rytteråker Formation is characterized as a bioclastic coarsening-upward sequence, passing up into a fining-upward sequence (Möller 1989). The coarsening-upward part of the formation is terminated through much of the Oslo Region by massive coarse bioclastic limestones or by coral–stromatoporoid bioherms and biostromes. Pentamerid brachiopods are common and frequently occur as in situ nests. The upper, fining-upward sequence is dominated by fine-grained bioturbated limestones. The upper boundary with the shales and nodular limestones of the overlying Vik Formation is fairly abrupt.

A disconformity surface is evident within the Rytteråker Formation of Asker and also in the Ringerike and Hadeland districts of the Oslo Region, with some erosion of the underlying limestone before carbonate deposition recommenced. Conditions following this hiatus appear to have been broadly similar to those preceding it.

Conodonts in the Oslo–Asker district

The conodont fauna of the Rytteråker Formation shows a low abundance and a low diversity (Aldridge & Mohamed 1982; Nakrem 1986). Not all samples have yielded conodonts, but new collections from Malmøykalven contain more than 50 specimens of *Panderodus*, including black, mostly broken, elements of *P. unicostatus* or *P. equicostatus* together with *P. recurvatus*. *Pseudolonchodina fluegeli* (Walliser) and elements of *Walliserodus* occur in small numbers, and occasional specimens of *Oulodus* sp., *Distomodus* sp. and *Ozarkodina* cf. *excavata* have been found.

Other biota in the Oslo–Asker district

Above the lowest 15 m, the formation is characterized by moderately diverse associations of corals, stromatoporoids, crinoids, brachiopods, trilobites and ichnofossils. Pentamerid banks and patch reefs occur. The facies is similar in the Ringerike district, where acritarch species diversity drops from around 20 to seven taxa in the middle of the formation (Smelror 1987).

Other areas

Coeval strata in Britain include the upper part of the Pentamerus Beds and the lowest part of the overlying Hughley Shales formation, which contain a slightly more diverse conodont fauna than found in Norway, with *D. staurognathoides* reasonably common, together with *O. aldridgei*, *O. excavata*, *O.* aff. *oldhamensis*, *Oulodus* spp., *P. fluegeli*, *P. equicostatus*, *P. recurvatus*, *Pseudooneotodus* sp., *Walliserodus* sp. and *Decoriconus fragilis* (Branson & Mehl) (Aldridge 1972, 1985). A reasonably diverse benthic macrofauna is associated, representing the *Pentamerus*, *Stricklandia* and *Clorinda* communities (Ziegler *et al.* 1968). Acritarchs are fairly diverse at this level in Shropshire (Hill 1974) and in the type Llandovery area (Hill & Dorning 1984).

In the Mackenzie Mountains, the late Aeronian conodont extinctions are followed by an impoverished fauna dominated by *P. fluegeli* and also containing *Dapsilodus*, *Panderodus*, *Walliserodus* and *Decoriconus* (Over & Chatterton 1987). On Anticosti Island, the collections through the upper part of the Jupiter Formation are a little more diverse; they lack *P. fluegeli*, but contain *O. aldridgei*, *D. staurognathoides* and *Oulodus* spp. (Uyeno & Barnes 1983). Brachiopods are particularly abundant in the same interval (Petryk 1981) and corals are diverse (Bolton 1981).

Low abundance and diversity of conodont collections between the last *O. hassi* and the first *Pterospathodus celloni* (Walliser) were also reported by Armstrong (1990) within the Odins Fjord Formation of North Greenland. Conodonts found within this interval include *P. fluegeli*, *K. manitoulinensis*, *O. pirata*, *O. excavata*, *Panderodus greenlandensis*, *P. unicostatus* and other species of

Panderodus (Armstrong 1990, figs 6,7,9 & 10). Hurst (1984) reported a rich shelly fauna from the same strata, with stromatoporoids and tabulate corals often very abundant, although in some places the bottom conditions may occasionally have been anoxic.

Interpretation

This interval shows all the characteristics expected of a secundo episode. Warm shelf seas with reduced clastic input led to widespread development of shelf carbonates, with corals and stromatoporoids abundant. Low planktonic productivity is suggested by the impoverishment of acritarch microfloras and of conodont faunas.

The Snipklint Primo episode

Name

After the cliff at Ireviken 3, Gotland (Laufeld 1974*b*), where the later part of the episode is well represented.

Boundaries

The beginning of the episode is represented close to the base of the *Pterospathodus celloni* Conodont Biozone; it coincided approximately with the first appearance of *P. celloni*, but the change from the Malmøykalven Secundo episode is gradational, and some characteristic species may have appeared slightly earlier. This level is within the *M. turriculatus* or *M. crispus* Graptolite Biozone. The episode spans much of the interval included in the *P. celloni* and *P. amorphognathoides* conodont biozones, extending to close to the Llandovery–Wenlock boundary, which approximates to the top of the British *M. crenulata* Graptolite Biozone. The end coincides with the beginning of the Ireviken event.

Lithological characteristics in the Oslo–Asker district

The episode is represented by the Vik Formation, which comprises greenish grey or red shales and marls with beds of finely nodular limestone (Worsley *et al.* 1983, Möller 1989). In the northern districts of the Oslo Region, the shales are dark, carbonate-poor and graptolitic (Möller 1989).

Lithological characteristics on Gotland

Only the later part of the episode is represented in strata exposed in cliff sections above sea level, but older parts have been cored. The dominant lithology is of grey marls and argillaceous nodular limestones. There is a distinct red layer immediately below the *P. celloni–P. amorphognathoides* biozonal boundary.

Conodonts in the Oslo–Asker district

Globally, the *P. celloni* and *P. amorphognathoides* biozones contain by far the greatest diversity and disparity of conodonts found in Silurian strata (Aldridge 1988). The fauna is dominated by species referred to the *Pterospathodus* Association (Aldridge & Jeppsson in press), characterized by a wide variety of taxa with platforms. This richness is quite well represented in the Oslo–Asker district, where *D. staurognathoides*, *P. celloni*, *P. amorphognathoides* Walliser, *Carniodus carnulus* Walliser,

Ozarkodina polinclinata Nicoll & Rexroad, *Aulacognathus bullatus* Nicoll & Rexroad, *Apsidognathus walmsleyi* Aldridge, *Oulodus petilus* (Nicoll & Rexroad), *P. fluegeli*, *P. tricornis*, *D. obliquicostatus*, *D. fragilis*, *P. unicostatus*, *P. recurvatus*, *Walliserodus* sp. and other species have been recorded (Aldridge & Mohamed 1982; Nakrem 1986). In the Malmøya section near Oslo, the lowest *P. celloni* has been found 30 m above the base of the Vik Formation; the lowest *D. staurognathoides* was found at 10 m and the lowest *A. bullatus* at 25 m (Nakrem 1986).

Conodonts on Gotland

The fauna of the *P. amorphognathoides* Biozone is dominated by the *Pterospathodus* Association and includes more than 20 conodont species (Fig. 2). Its abundance, disparity and diversity are second to no other interval on Gotland. As well as containing characteristic platform-equipped taxa, including *P. amorphognathoides*, *D. staurognathoides* and *A. walmsleyi*, collections show a wide variety of species of *Panderodus*, which is represented by *P. unicostatus*, *P. serratus*, *P. recurvatus*, *P. langkawiensis*, *P. greenlandensis* and a new species.

Other biota in the Oslo–Asker district and on Gotland

Graptolites continue to be uncommon in the Oslo–Asker district, although some are known from the upper Llandovery Skinnerbukta Formation. Further north in the Oslo Graben, however, the Ek Formation contains several thin graptolite-rich horizons representing the *M. turriculatus* to *M. crenulata* biozones (Howe 1982). In the Ringerike district, acritarchs show a diversity peak encompassing the upper part of the Vik Formation and the lower part of the Bruflat Formation (Smelror 1987). Brachiopods contrastingly show a diversity drop within the same strata (Cocks & Baarli 1982).

The Lower Visby Beds of Gotland have a very rich shelly fauna, with diverse brachiopods, trilobites, bryozoans, corals, conulariids and other fossils. Chitinozoans are very abundant (Laufeld 1974a), and acritarch assemblages are of high diversity (Le Hérissé 1989). Graptolites are rare as complete fossils, but many fragmentary specimens have been found during conodont extraction.

Other areas

In Britain, the first *P. celloni* occur low in the Hughley Shales of Shropshire (locality of sample Sheinton 2 of Aldridge 1972, p. 141), where associated taxa include *D. staurognathoides*, *P. fluegeli*, *O. aldridgei*, *Kockelella* aff. *ranuliformis* (Walliser), *O. excavata*, *Oulodus* spp., *P. equicostatus*, *P. serratus*, *P. recurvatus*, *Pseudooneotodus tricornis* Drygant, *W. curvatus* and *D. fragilis* and rare specimens of *Icriodella* sp. nov. (Aldridge 1972, 1985). Higher in the *P. celloni* Biozone, *O. aldridgei* disappears, but several characteristic platform genera join the fauna, including *Astropentagnathus irregularis* Mostler, *Aulacognathus kuehni* Mostler, *A. bullatus* (Nicoll & Rexroad), *Apsidognathus tuberculatus* Walliser and *Icriodella inconstans* Aldridge. *Ozarkodina gulletensis* is also common in the lower part of the zone, but becomes rare in the middle and disappears before the top. Conodont faunas throughout the *P. celloni* and *P. amorphognathoides* biozones are very diverse and disparate, with up to 30 species present at any one time, and samples commonly

contain abundant specimens. Other fossils, including brachiopods, solitary rugose corals, trilobites and ichnofossils are also common and varied at some horizons (e.g. Cocks & Walton 1968). Acritarch diversity is moderate to high, although abundance is rather variable. In general, western European acritarch assemblages are of high diversity at this level. Graptolites show a diversification in the lower part of the *M. turriculatus* Biozone, followed by extinctions in several lineages in the middle of the zone; a lower but reasonable diversity persists for the rest of the Telychian (Loydell 1993, pers. comm.).

On Anticosti Island, characteristic conodont species of the Snipklint Primo episode, including *A. bullatus*, *I inconstans* and *A. irregularis* begin to appear in the uppermost lime mudstones of the Jupiter Formation (Uyeno & Barnes 1983). The appearance of *P. celloni*, together with *A. tuberculatus* and *C. carnulus*, coincides with the incoming of crinoidal grainstones at the base of the Chicotte Formation. In the deeper water sediments of the Mackenzie Mountains, a fauna dominated by *Panderodus*, *Astropentagnathus*, *Aulacognathus* and *Pterospathodus* appears at the base of Member 3W of the Whittaker Formation (Over & Chatterton 1987). The underlying Member 2W, representing the Malmøykalven Secundo episode, comprises dark, thinly laminated dolomites and dolomitic cherts, with the only fossils recognized being thin shells and radiolarian ghosts. The argillaceous micrites, shales and cherts of Member 3W contain, in addition to the conodonts, common articulate and inarticulate brachiopods, trilobites, conulariids, ostracodes and radiolarians (Over & Chatterton 1987, p. 5).

In New South Wales, Australia, Bischoff (1986, fig. 10) found low diversity conodont faunas in strata referred to the *M. sedgwickii* and *M. turriculatus* graptolite biozones, although coniform taxa were not included in his coverage. A feature of the Australian faunas, however, is the presence of small numbers of early species of *Aulacognathus* in these beds. The first *Pterospathodus* appear in strata assigned to the *M. crispus* Graptolite Biozone, along with *Apsidognathus*, *Astropentagnathus* and other taxa. This diversification continues into the *M. griestoniensis* Biozone, coincident with a decrease in carbonate sedimentation, and rich faunas persisted to the end of the episode.

In many areas where late Llandovery conodont faunas have been studied there is a distinct correlation between the occurrence of the rich faunas of the Snipklint Primo episode and the deposition of clastic sediments in environments previously and/or subsequently characterized by carbonates. This relationship has been fully documented elsewhere for that part of the episode referable to the *P. amorphognathoides* Biozone (Jeppsson 1987). A widespread occurrence of marine red beds in the Telychian has also been documented by Ziegler & McKerrow(1975).

Interpretation

Increased humidity led to an increase in weathering, run off, and deposition of argillaceous sediments. Nutrient supply was also enhanced leading to high planktonic production, which supported abundant and diverse communities. The lowered temperatures and more turbid and nutrient-rich waters were detrimental for benthic carbonate production and net deposition decreased in marginal carbonate areas. Oceanic waters were, however, better oxygenated, allowing infaunal and epifaunal benthic organisms to survive in places

where they were formerly rare due to low levels of oxygen and/or food. Thus calcareous horizons may be found in sequences which otherwise lack indigenous biogenic carbonate.

Although conditions were similar throughout the Snipklint Primo episode, at least two subdivisions can be recognized, each with a characteristic fauna and microflora. The very high diversities in all groups during this interval may indicate that this was the first return to full cycling of nutrients after the late Ordovician glaciation, producing bonanza conditions, especially for plankton and plankton-dependent communities.

The Ireviken P–S event

Name

Named by Jeppsson (in press) after locality Ireviken 3, on the west side of the bay at Ireviken, Gotland (see Laufeld 1974b).

Boundaries and datum points

The beginning of this event is represented in the uppermost *P. amorphognathoides* Biozone at the point where the ratio between *Pseudooneotodus tricornis* and *P. bicornis* decreases dramatically, with the former disappearing completely in most reported sections. The end coincided with the beginning of the Vattenfallet Secundo episode. Eight datum points can currently be recognized to span the event on the basis of turnover in the conodont faunas throughout the reference area (Fig. 2). In ascending order these are as follows.

(1) The beginning of the event, at which point *P. tricornis* and an undescribed species with coniform elements disappeared. A new species of *Ozarkodina* also disappeared, but returned before the end of the event. *Kockelella ranuliformis* and *P. bicornis* reappeared after a considerable absence.

(2) This datum shows the most significant conodont changes within the Ireviken event, with the extinctions of *Apsidognathus, O. polinclinata* and *P. fluegeli*. *Panderodus greenlandensis* disappeared temporarily, and *O. petilus* made a brief disappearance until datum 4. *P. equicostatus* reoccurred.

(3) The extinction of *P. amorphognathoides*.

(4) This datum coincides with the boundary between the Lower and Upper Visby Beds. *Oulodus petilus* and *Ozarkodina* sp. nov. became extinct, *P. serratus* disappeared and *Ozarkodina* aff. *confluens* (=*Hindeodella* aff. *confluens* of Jeppsson 1979) appeared.

(5) The disappearance of *Walliserodus curvatus*.

(6) The extinction of *Pterospathodus*. The last populations of this genus, after the extinction of *P. amorphognathoides*, are diminutive and resemble juveniles of *P. amorphognathoides* and *P. procerus*; larger specimens are closer to *P. procerus*, so we refer all the specimens to that species.

(7) The extinction of *D. staurognathoides*.

(8) The disappearance of *P. unicostatus*. This occurs close to, or at the contact between the Upper Visby Beds and the Högklint Beds.

In terms of the graptolite biozonation, the Ireviken event probably ranges from within the *M. spiralis* Biozone,

through the *C. centrifugus* (*C. insectus*) Biozone and into or through the *C. murchisoni* Biozone. In chronostratigraphical terms, the base of the event is very close to the Llandovery–Wenlock boundary. At the boundary stratotype section at Leasows, Shropshire, the last *P. tricornis* occurs immediately above the base of the Wenlock, to be followed within 25 cm by the extinctions of *P. langkawiensis, C. carnulus, D. staurognathoides* and *P. amorphognathoides* (Mabillard & Aldridge 1985); the sequence at this locality may, however, be complicated by minor faulting.

Lithological characteristics on Gotland

The uppermost Lower Visby Beds are similar to those of the Snipklint Primo episode, although the trend towards more calcareous sedimentation continued. The Upper Visby Beds consist of argillaceous limestones with small reefs.

Conodonts on Gotland

The effects at the first datum were minor, but those at the second datum were very pronounced. In addition to the extinctions and disappearances noted above, total abundance decreased and the relative frequencies of different taxa changed, with lowered numbers of those species that were to succumb at the fourth datum. After the extinction of *P. amorphognathoides*, faunas are dominated by *P. equicostatus, P. serratus* and *P. unicostatus*.

Other biota on Gotland

There was a major effect on trilobites at the second datum, where ranges recorded at locality Rönnklint 1 show that at least half the species disappeared (Ramsköld 1985, p. 4). The coral *Paleocyclus porpita* became extinct at the fourth datum. Two of five paulinitid polychaetes present during the Snipklint Primo episode became extinct during the event (Bergman 1989), one at or close to the first datum. The fourth datum had a strong affect on beyrichiid ostracodes with five of ten species becoming extinct and three new species appearing (Martinsson 1962, 1967).

Acritarchs show a very marked decrease in diversity through the Upper Visby Beds and lowermost Högklint Limestone (Le Hérissé 1989), though sampling was insufficiently detailed to detect the pattern of extinctions.

Other areas

The event affected conodont faunas globally, and several of the datum points can be widely identified, for example in Australia (Bischoff 1986) and Alaska (Savage 1985). In Britain, the event is represented in the Wenlock type area (see above), but is better revealed in unpublished collections from the BGS Eastnor Park Borehole in the Malvern Hills. Here, a sequence of extinctions affects *P. tricornis* (highest occurence at a depth of 55.3 m), *P. fluegeli* (55.3 m), *A. tuberculatus* (50.1 m), *P. recurvatus* (47.8 m), *P. amorphognathoides* (coincidentally with *P. langkawiensis* at 43.8 m), *D. staurognathoides* (43.2 m), and diminutive *P. procerus* (42.1 m). Although the size of the borehole collections is necessarily smaller than desirable (hundreds rather than thousands of specimens), the pattern of events shows a close match to that identified on Gotland (Fig. 3).

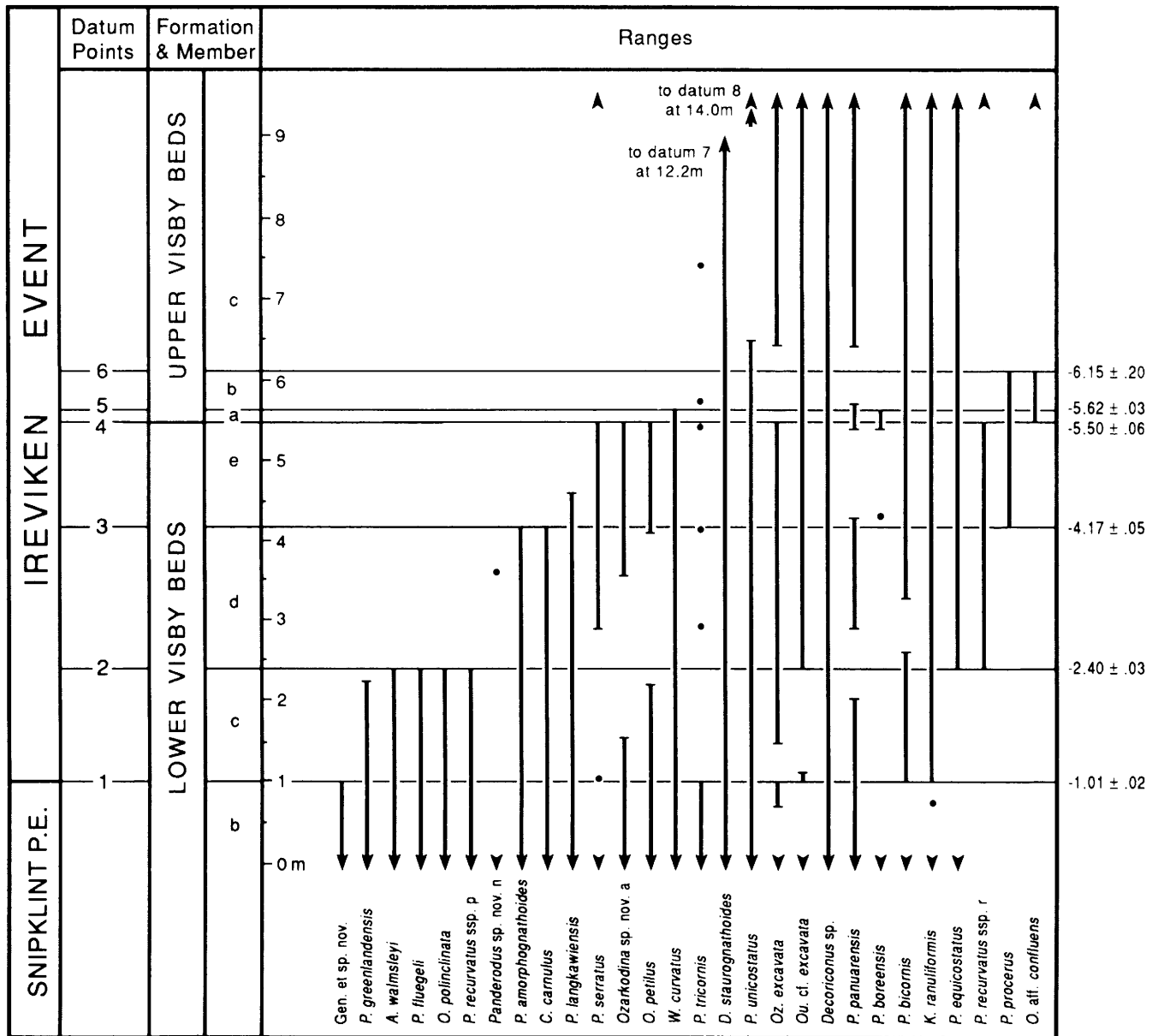Documentation is not generally sufficiently detailed to determine the extent to which other organisms were

Fig. 2. Conodont ranges at Ireviken 3, Gotland, indicating the positions of the eight datum points. Measurements to the right give precise positions of the datum levels in metres above a reference bentonite at 0m.

affected, but there is evidence of extinction and turnover in several groups. At the Leasows section, Shropshire, for example, the diversity of agglutinated foraminifera and of ostracodes drops markedly above the base of the Wenlock, while acritarch diversities fluctuate considerably through the event (Mabillard & Aldridge 1985). Range charts for graptolites in Britain also show a changeover at the boundary between the *M. crenulata* and *C. centrifugus* biozones and a very marked diversity drop in the *C. murchisoni* Biozone (e.g. Rickards 1976). Boucot (1991), in a brief summary of Silurian bioevents, also noted 'relatively contemporaneous' extinctions in trilobites (several lineages), brachiopods (the *Stricklandia* and *Eocoelia* lineages) and pelmatozoans.

Interpretation

Jeppsson (1990, p. 668, in press) discussed in detail how transitions from a P-state, with temperature-dense bottom water, to an S-state, with salinity-dense bottom water, would span a geologically detectable period of time during which slight climatic changes could produce major effects on oceanic circulation. Instead of a steady transition, the event was prolonged by a number of Milankovitch-generated brief returns to P-state conditions, between which no new bottom water was produced and deep upwelling was very low. One result was that faunas were repeatedly stressed, leading to stepwise extinctions.

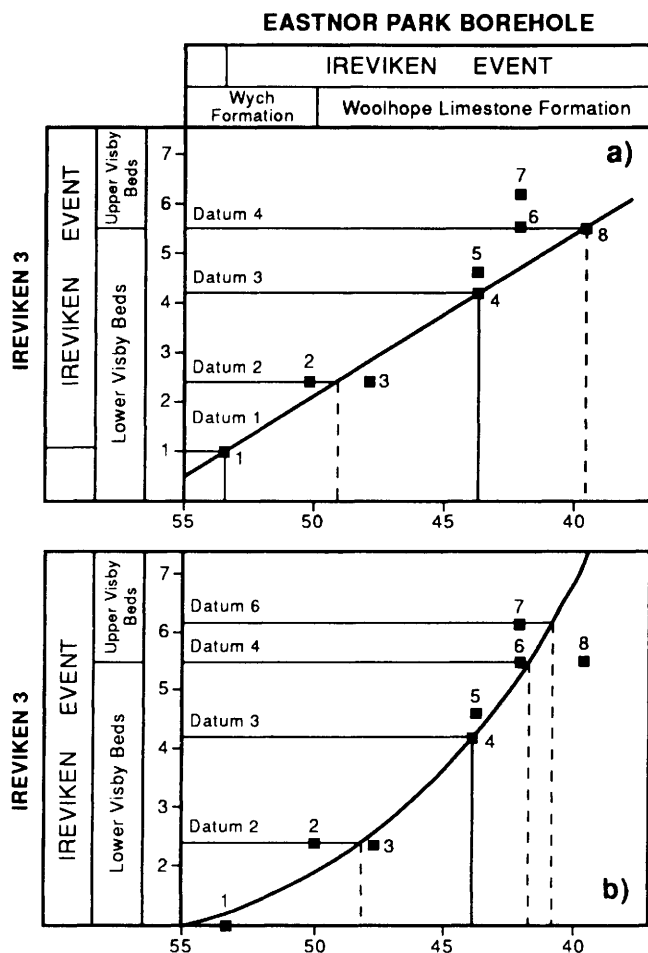The pattern of conodont extinctions during the Ireviken

Fig. 3. Graphical comparison of the Ireviken 3 section with the Eastnor Park Borehole using the following points: 1, top of *P. tricornis*; 2, top of *Apsidognathus*; 3, top of *P. recurvatus* subsp. nov.; 4, top of *P. amorphognathoides*; 5, top of *P. langkawiensis*; 6, top of *P. serratus*; 7, top of *P. procerus*; 8, bottom of *O.* aff. *confluens*. (a) Straight line of correlation (assuming constant relative rates of sedimentation) anchored at points 1 and 4, judged to be the most reliable on numbers of specimens. (b) Exponential curve fitted graphically to all points. Scale in metres; for Ireviken 3 measurements are given above the reference bentonite, for the Eastnor Park Borehole the figures are depths.

event is neatly explained by this model. Conditions during the Snipklint Primo episode had allowed the development of very high diversity faunas, characterized by specialized taxa, which were particularly vulnerable to changes in nutrient supply and planktonic productivity. These changes precipitated an extinction event that is clearly the sum of several minor events separated by short intervals of time. As noted by Jeppsson (1990, in press) calculations based on stratal thicknesses in Gotland suggest that the separation of these minor events is consistent with a control related to the Milankovitch obliquity term.

Conclusions

Patterns of extinction, radiation and replacement in early Silurian conodonts are explained well by a model involving cyclic changes in climatic and oceanic state. The changes in conodont faunas were commonly coeval with widespread

changes in sedimentation and in other biota that are largely consistent with the model for P and S cycles proposed by Jeppsson (1990). We have, therefore, proposed a set of named P (primo) and S (secundo) episodes, using the well-exposed and well-documented successions in the Oslo Graben and on Gotland as reference areas. The pattern we have documented, and the model we have adopted to explain it, are open to independent testing on other lower Silurian successions. Not all sections will show a typical set of changes, as local environmental and tectonic effects will have overprinted the global episodicity; however, some effects of the episodes and events should be recognizable coevally in all regions. In addition, the model makes predictions about black shale distribution in oceanic deposits and about $\delta^{13}C$ excursions during primo and secundo episodes that we have been unable to test using existing data. Precise correlations between oceanic and shelf successions need to be established as a prerequisite for determining whether oxic/anoxic signals in oceanic strata correspond directly with shale/carbonate changeovers on the shelf.

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